

A quantitative comparison of hectocotylus morphology between Mediterranean and western Atlantic populations of the squid *Illex coindetii* (Mollusca: Cephalopoda: Oegopsida: Ommastrephidae)

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Abstract.—Geographic variation in morphology of the commercially important squid species *Illex coindetii* has led to speculation about possible taxonomic differences among populations. We compared hectocotylus morphology between western Atlantic specimens, from the Gulf of Mexico and Caribbean, and Mediterranean specimens, from the Tyrrhenian Sea. Although a few differences were found in morphometrics and meristics, we conclude that the two populations are conspecific.

Although *Illex coindetii* is important to fisheries, systematic questions about relationships among populations referred to this species remain unresolved. Several authors disagree on the number of species-level taxa of the genus *Illex*. This is due primarily to the presence of several different "morphs" that are difficult to assign to a recognized species (Zuev 1966, Aldrich & Lu 1968). Indeed, various morphological clines exist among the different species of *Illex*, especially in the area off the southeastern United States where distributions of three species overlap (Roper et al. 1996).

Until Roper et al. (1969) recognized *Illex coindetii* in the western North Atlantic, all *Illex* in that region had been referred to *I. illecebrosus*. Other cephalopod researchers, such as G. L. Voss, were reluctant during the 1970s and 80s to accept multiple species of *Illex* in the western North Atlantic (K. Mangold, pers comm). Nesis (1987) listed *argentinus*, *illecebrosus* and *coindetii* as subspecies of *I. illecebrosus*. Whereas Nesis (1987) recognized only *I. illecebrosus* and *I. oxygonius* as full species, Chin-

gus Nigmatullin considers *I. illecebrosus*, *I. coindetii* and *I. argentinus* to be valid species, but *oxygonius* to be a reproductive morph found in all *Illex* species (pers. comm. Also see e.g., fig. 1 in Laptikhovsky & Nigmatullin 1993).

Illex coindetii inhabits the continental shelf and upper slope. Its distribution as currently defined is very broad, ranging from the eastern to the western Atlantic. The species can be found along the European coast of the Atlantic Ocean, from Oslo Fjord and the North Sea (ca. 59°N), to the Bristol Channel southward; the Mediterranean, Adriatic and Aegean seas; and the Atlantic coast of Africa as far south as Namibia (19–20°S). The species is absent from the upper Adriatic Sea and the Black Sea. In the western Atlantic *I. coindetii* lives from 37°N through the Florida Straits, Gulf of Mexico, Caribbean Sea, to north-eastern South America, including Venezuela, Surinam and French Guiana (ca. 3°N). According to Roper et al. (1996), multiple morphs of *Illex coindetii* occur in both the eastern and western Atlantic, but all appear

to be conspecific. Although Roper et al. (1996) compared specimens of *I. coindetii* from both sides of the Atlantic, they did not include detailed quantitative analyses.

An alternative explanation for the disjunct distribution of *I. coindetii* is that eastern and western Atlantic populations now considered to be *I. coindetii* are separate species, with gene flow interrupted by the spreading of the Atlantic since the end of the Cretaceous. Because this species has never been reported from mid-ocean samples, gene flow between eastern and western Atlantic populations now may be limited or non-existent. Therefore, allopatric processes may have allowed genetic divergence to occur between these populations.

Hectocotylus morphology includes several characters that are among the most important for definition of the species of *Illex*, and they were used by Roper and Mangold (1997) to redefine *I. coindetii*. As part of a larger study of development of the hectocotylus in *I. coindetii*, we examined meristics and morphometrics of hectocotylus characters in specimens from the Gulf of Mexico/Caribbean Sea area of the western North Atlantic and from the Tyrrhenian Sea in the Mediterranean to determine whether any differences are equivalent to those used to distinguish among other species of *Illex*.

Materials and Methods

Twenty-seven adult male specimens were examined both from the North Tyrrhenian Sea and from the region of the Gulf of Mexico and Caribbean Sea.

Tyrrhenian specimens were obtained from two samples taken from commercial catches landed at Porto S. Stefano, Grosseto, Italy. The first sample was caught in November 1992, the second sample in May 1993. Specimens were fixed in formalin/seawater as recommended by Roper & Sweeney (1983). Then they were drained, rolled in cheesecloth (lightly soaked in a 7% solution of formalin), and shipped to the National Museum of Natural History

(NMNH) in Washington, D.C. Upon arrival, the specimens were transferred into 45% isopropyl alcohol.

Specimens from the Gulf of Mexico and Caribbean Sea came from the NMNH collections and from the Marine Invertebrate Museum of the University of Miami's Rosenstiel School of Marine and Atmospheric Science (RSMAS) in Miami, Florida. All had been fixed in formalin. Specimens from NMNH had been preserved in 45% isopropyl alcohol whereas those from RSMAS were in 70% ethanol for varying lengths of time. Specimens from these collections were selected to equal the number of mature males from the Tyrrhenian Sea, based on sex, maturity, collecting location, and physical condition.

For the present work, only mature males were selected. The maturity scale used was modified from that of Lipinski (1979); a fully mature male has the Needham's sac swollen with spermatophores and the testis at its maximum development.

Measurements.—We examined the following characteristics: mantle length; the basal section of the hectocotylized arm, which has no suckers; the proximal section of the hectocotylized arm, which has normal suckers; the medial section of the hectocotylized arm, which has reduced suckers and fringed trabecular flaps; the distal section of the hectocotylized arm and its major modifications, lamellae and papillae; and the dentition of the suckers.

Most measurements were made with a flexible ruler. The diameter of the suckers and number of tiny suckers on the tip of the hectocotylus were assessed using a dissecting microscope with an ocular micrometer.

Statistical comparisons used the Tukey-Kramer method (Sokal & Rohlf 1981) to compare averages of measurements, indices, and counts of the two populations. Linear regressions were compared to evaluate differences between relationships of the measured characters with ML. The following abbreviations were used: ML: Dorsal mantle length; HALt: total length of hec-

tocotylyzed arm from proximal V-notch to distal tip (see Fig. 1); OALt: total length of opposite arm from proximal V-notch to distal tip; HAb: length of hectocotylyzed arm from V-notch to the first (most proximal) sucker—This is the basal, suckerless part of the arm; HA1: length of proximal region of hectocotylyzed arm, bearing normal suckers; HA2: length of medial region of hectocotylyzed arm, bearing reduced suckers and fringed trabecular flaps; HA3: length of distal hectocotylyzed arm tip, bearing lamellae and papillae; HASn: greatest diameter of exposed part of horny ring of normal suckers on HA1; HASr: greatest diameter of exposed part of horny ring of reduced suckers on HA2; HA1SC: number of suckers on HA1; HA2SC: number of suckers on HA2; LC: number of lamellae on HA3; (this includes, unless otherwise specified, the number of knobs present on the lamellae row); PC: number of papillae (and knobs) on HA3; HALti: index of HALt as percentage of ML; OALti: index of OALt as percentage of ML (note that this index and HALti are the only ones standardized to ML); XXXi: index of the measure XXX (e.g., HAb) as percentage of HALt; R: correlation coefficient of the linear regression.

Results

Basic modifications of the hectocotylyzed arm are similar in both populations. Either the right or left ventral arm is hectocotylyzed. It is longer (about 4–5%) and more robust than the opposite arm. The hectocotylyzed tip (HA3) is about 26% (\pm ca. 3%) of the length of the hectocotylyzed arm. Distal to the proximal 7th normal pair, the suckers diminish in size and the trabeculae are modified into 10–14 lobate flaps that are fringed and papillose (HA2). The second or third pair of modified trabeculae are the largest; distally, they are reduced in size. Suckers and protective membranes are not found on the modified tip (HA3). In the dorsal row of HA3, 1–2 conical knobs are followed by a series of transversely broad,

thin, nearly truncate flaps or lamellae that gradually reduce in size distally. Minute papillae occur on the distal tip. In the ventral row of HA3, there is a series of conical papillae that gradually diminish in size toward the tip of the arm. A low, weak zigzag ridge is sometimes visible between papillae and lamellae. The aboral keel is broadly expanded along the distal portion of the hectocotylyzed arm (HA3).

Quantitative observations.—Statistical comparisons of measurements, counts, and indices are summarized in Tables 1–3. Average measurements show that the specimens from the western Atlantic are larger than those from the Mediterranean. The larger western Atlantic squids have longer arms, both hectocotylyzed and opposite, and larger suckers than those from the Mediterranean, although relative to ML the arms of western Atlantic squids were shorter. Regression analysis (Fig. 2), showed that all of these characters overlapped greatly when considered as a function of overall size of the specimens (ML).

Sucker counts do not differ significantly between populations, although western Atlantic squids tend to have one sucker more in the medial section (HA2) and one fewer in the proximal section (HA1) than in the Mediterranean squids. There are significantly fewer papillae in the Tyrrhenian specimens and the reduction in number of lamellae in the Tyrrhenian specimens is highly significant.

The differences in indices between populations are not statistically significant except for the length of the opposite arm. In Tyrrhenian specimens the non-hectocotylyzed ventral arm is longer relative to the mantle length than in western Atlantic specimens. Although not statistically significant, a similar trend is seen in the relative lengths of the hectocotylyzed arms. It is important to remember, though, that finding a significant difference in one of several analyses can result from random effects, resulting in incorrect rejection of a true null hypothesis (no difference). Thus, a conservative inter-

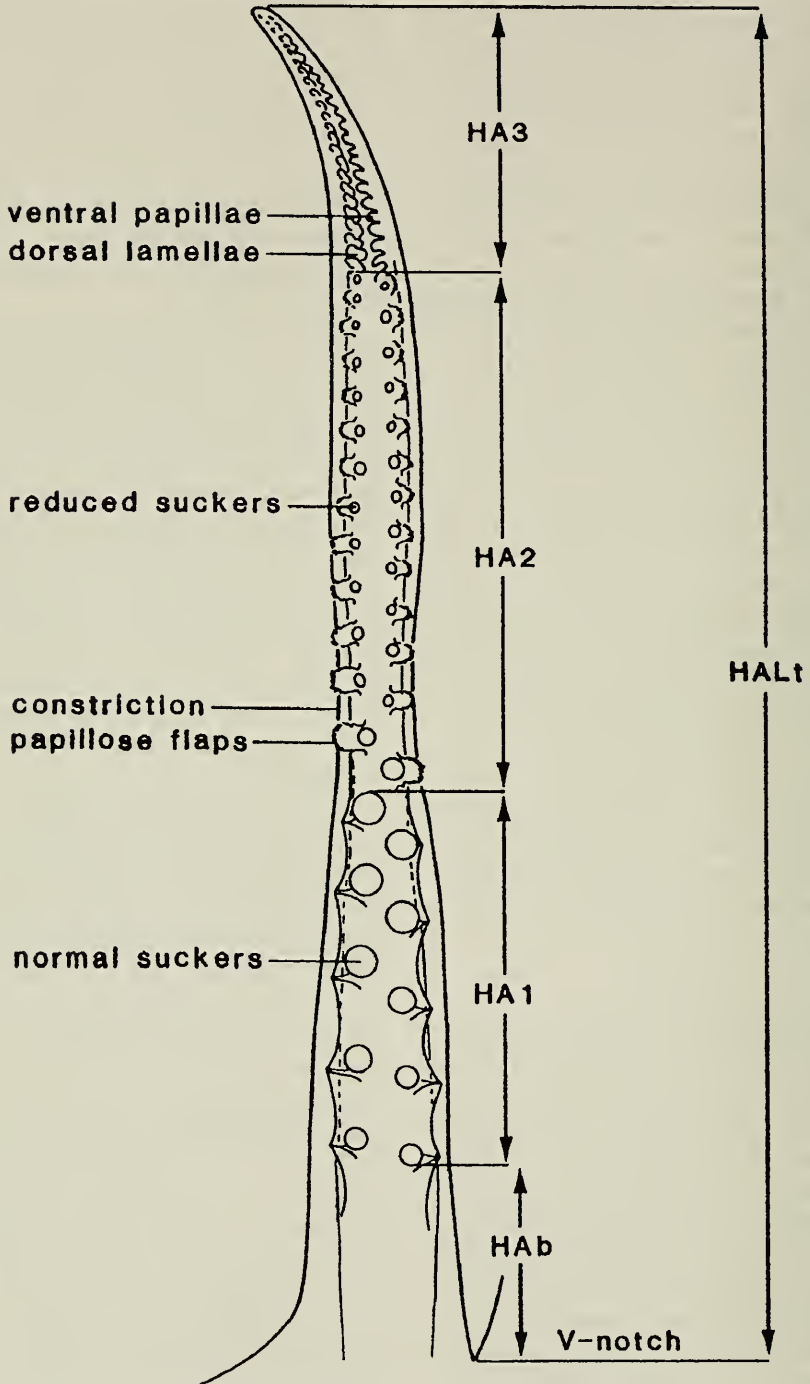


Fig. 1. The hectocotylus of *Illex coindetii* and its parts; knobs are not represented. Slightly modified from Roper & Mangold (1997).

Table 1.—Comparison of measurements (in mm) between *Illex coindetii* from the Tyrrhenian Sea (TYR) and from the Gulf of Mexico/Caribbean Sea (MEX). Mean values are presented along with standard deviation and the probability that there is no difference between the populations.

Measurement	TYR	MEX	Probability
ML	131.23 ± 19.88	148.33 ± 16.75	$P = 0.001$
OALt	87.89 ± 13.03	95.11 ± 9.94	$P = 0.025$
HALt	92.16 ± 12.01	98.63 ± 10.49	$P = 0.038$
HAb	9.63 ± 2.22	10.37 ± 2.02	$P = 0.199$
HA1	26.21 ± 5.61	28.33 ± 4.67	$P = 0.135$
HA2	31.95 ± 4.94	34.37 ± 4.74	$P = 0.069$
HA3	24.41 ± 4.77	25.93 ± 3.33	$P = 0.179$
HASn	1.845 ± 0.313	2.016 ± 0.297	$P = 0.043$
HASr	0.556 ± 0.163	0.625 ± 0.138	$P = 0.304$

pretation of the analyses of indices is that the two populations are not different.

As a rule, in the comparison of linear regressions for relationships between measures and mantle length (Table 4), the western Atlantic specimens show more variance in the vertical-axis coefficient than do the Mediterranean ones. In general, the slopes of the regressions are steeper for Tyrrhenian specimens, than for western Atlantic ones. This means that for the same increase in length of the mantle, the arms or their parts generally grow more in Mediterranean specimens. The only exception is HAb, the suckerless basal region of the hectocotylus. This shows a higher slope (faster growth) in specimens from the Gulf of Mexico/Caribbean Sea.

Qualitative differences.—Specimens from the Gulf of Mexico/Caribbean have modifications on the hectocotylized arm

that show a greater degree of development and usually are relatively larger than in the Tyrrhenian specimens. For example, the development of fringed flaps is greater in western Atlantic specimens. However, the flaps diminish in size gradually toward the tip of the arm in specimens from both areas. Papillae in the ventral row are longer and set along the ventral side of a zigzag ridge always present on the hectocotylus in animals from the Gulf of Mexico/Caribbean. The dorsal row of lamellae usually has one or two knobs, although sometimes there are no knobs and rarely there are 3 or 4 knobs. No specimens from the Mediterranean had four knobs. The suckers have the same kind of dentition in both geographic areas.

Squids from the Gulf of Mexico/Caribbean have papillae and lamellae that are more similar in numbers, because of the presence of the zigzag ridge connecting the lamellae dorsally and papillae ventrally. The zigzag ridge is very rare in Tyrrhenian specimens, and when present its shape usually is not so well defined. This seems to be related to the higher variability in numbers of papillae in the Mediterranean squids.

Table 2.—Comparison of counts of meristic characters of hectocotylized arms between specimens of *Illex coindetii* from the Tyrrhenian Sea (TYR) and from the Gulf of Mexico/Caribbean Sea (MEX). Mean values are presented along with standard deviation and the probability that there is no difference between the populations.

Meristic	TYR	MEX	Probability
HA1SC	11.96 ± 1.45	11.42 ± 1.30	$P = 0.156$
HA2SC	23.29 ± 3.62	24.15 ± 3.04	$P = 0.346$
PC	20.36 ± 8.51	25.15 ± 5.18	$P = 0.016$
LC	19.71 ± 5.22	24.19 ± 5.68	$P = 0.004$

Discussion

All species of the genus *Illex* possess hectocotyls with the same basic structure, i.e., the primary modification is the tip of the hectocotylized arm (HA3). Only this

Table 3.—Comparison of morphometric indices of *Illex coindetii* from the Tyrrhenian Sea (TYR) and from the Gulf of Mexico/Caribbean Sea (MEX). Mean values are presented along with standard deviation and the probability that there is no difference between the populations.

Index	TYR	MEX	Probability
OALti	67.67 ± 5.95	64.55 ± 5.25	<i>P</i> = 0.044
HALti	71.26 ± 7.15	66.76 ± 5.47	<i>P</i> = 0.177
HAbi	10.47 ± 2.35	10.44 ± 1.68	<i>P</i> = 0.096
HA1i	28.46 ± 4.48	28.69 ± 3.27	<i>P</i> = 0.823
HA2i	34.66 ± 3.10	34.84 ± 3.01	<i>P</i> = 0.829
HA3i	26.29 ± 3.19	26.32 ± 2.51	<i>P</i> = 0.970
HASni	2.008 ± 0.280	2.020 ± 0.281	<i>P</i> = 0.874
HASri	0.606 ± 0.169	0.634 ± 0.128	<i>P</i> = 0.493

part, with major modifications of sucker stalks into lamellae, knobs, and papillae, should be considered the true hectocotylus. The opposite arm shows no signs of hectocotylization. The opposite arm is shorter than the hectocotylized arm in all *Illex* species except *Illex illecebrosus*, in which the opposite arm is longer than the hectocotylized one. The mean, range, and standard deviation of ratio of length of the hectocotylus tip to the total length of the hectocotylized arm is (according to Roper et al. 1996): 13.0–22.1–30.3% ± 4.6% in *Illex illecebrosus*, 17.1–25.1–30.0% ± 2.7% in *I. coindetii*, 23.8–28.8–32.0% ± 2.7% in *I. oxygonius*, 19.8–50.3–70.3% ± 11.0% in *I. argentinus*.

Illex coindetii is the only species of this genus in which the medial part of the hectocotylized arm (HA2) forms a distinctive section. The medial section in *I. argentinus* is indistinguishable from the tip, resulting in the high ratio of tip length to arm length listed above. The medial section is unmodified in both *I. illecebrosus* and *I. oxygonius*. In *I. coindetii*, distal to the 7th pair of suckers the trabeculae (i.e., the fingerlike appendages from the sucker bases) are transformed into papillose fringed flaps. This feature, along with the reduction of sucker size, and the dentition of the horny rings of the suckers, is distinctive of the medial part of the hectocotylized arm (Lu 1973).

According to Lu (1973), the modified

trabeculae and flaps are larger and more papillose in *Illex coindetii* specimens from African waters (primarily the Gulf of Guinea) than in specimens from the Gulf of Mexico, the Caribbean Sea or the Mediterranean Sea. The length of the hectocotylized arm is different in these diverse areas; the Mediterranean Sea has animals with the longest hectocotylized arms, 71.1% of the mantle length, compared with 68.8% from the Caribbean Sea, 59.7% from the Gulf of Mexico, and 58.6% in those from West Africa.

Besides the presence of the more developed zigzag ridge on the tip of the hectocotylus in the western Atlantic specimens, no major differences have been detected between samples from the two study areas. We confirm that animals from the Gulf of Mexico/Caribbean Sea have relatively shorter hectocotylized and opposite arms, but this seems to be a general feature of all arms in this species in these areas. The number of suckers on the arm is approximately equal on animals from both areas, usually 10–14 suckers on HA1, 22–26 suckers on HA2. Considering that relative length of the tip of the modified arm is one of the key characters distinguishing the species of *Illex*, the two populations should be considered as belonging to the same species because the HA3i is not significantly different between areas.

Morphological variability across the broad geographic range of *I. coindetii* and

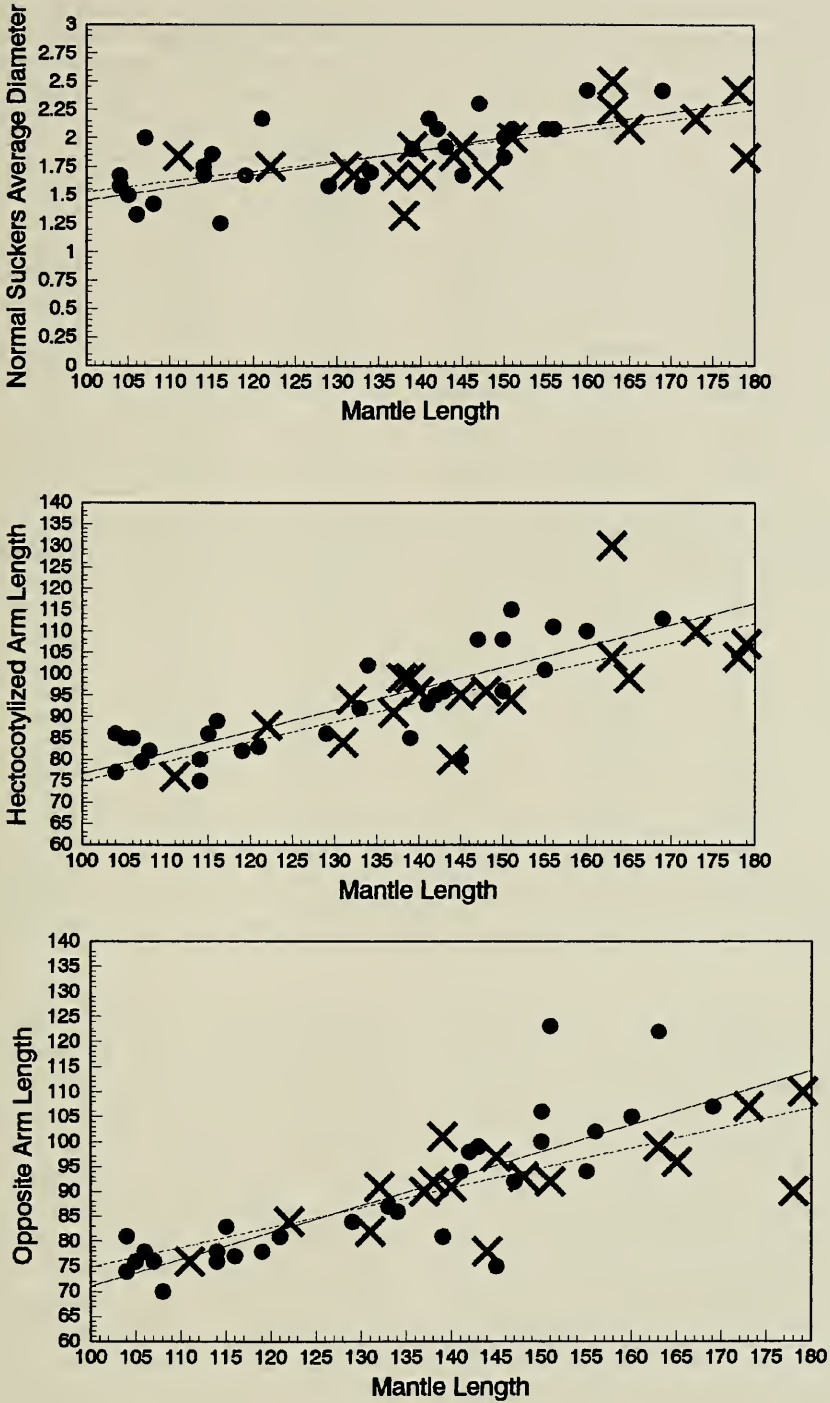


Fig. 2. Regressions of various measurements against mantle length. The graphs here are for the three measurements for which statistically significant differences were shown in Table 1. X = Gulf of Mexico/Caribbean specimens; ● = Tyrrhenian Sea specimens.

Table 4.—Linear regression indices with standard errors (SE) for morphometric and meristic characters regressed against mantle length. TYR, Specimens from the Tyrrhenian Sea in the Mediterranean; MEX, Specimens from the Gulf of Mexico and Caribbean; m, slope; q, vertical-axis intercept; R , correlation coefficient.

Character	TYR						
	m	SEm	q	SEq	R^2	R	$P_R > 0.95$
OALt	0.539	0.073	17.150	9.718	0.675	0.822	Y
HALt	0.498	0.067	26.777	8.903	0.680	0.825	Y
HAb	0.029	0.021	5.867	2.813	0.066	0.257	N
HA1	0.103	0.052	12.668	6.838	0.133	0.365	N
HA2	0.205	0.027	5.030	3.648	0.682	0.826	Y
HA3	0.160	0.035	0.035	3.355	0.669	0.818	Y
HA1Sn	0.011	0.002	0.351	0.282	0.524	0.724	Y
HA2Sr	0.002	0.002	0.243	0.204	0.085	0.292	N
HA1SC	-0.036	0.012	16.699	1.658	0.243	0.493	Y
HA2SC	0.062	0.034	15.156	4.458	0.116	0.341	N
PC	0.205	0.074	-6.606	9.777	0.230	0.480	Y
LC	0.126	0.055	2.501	7.366	0.166	0.407	Y
Character	MEX						
	m	SEm	q	SEq	R^2	R	$P_R > 0.95$
OALt	0.399	0.109	34.944	16.274	0.455	0.675	Y
HALt	0.460	0.109	29.006	16.300	0.525	0.725	Y
HAb	0.071	0.023	0.052	3.438	0.372	0.610	Y
HA1	0.202	0.053	-1.379	7.914	0.474	0.688	Y
HA2	0.069	0.055	22.851	8.176	0.091	0.302	N
HA3	0.110	0.039	9.276	5.840	0.330	0.574	Y
HA1Sn	0.009	0.003	0.629	0.376	0.434	0.659	Y
HA2Sr	0.003	0.001	0.218	0.217	0.157	0.396	N
HA1SC	0.012	0.016	10.021	2.324	0.035	0.187	N
HA2SC	0.021	0.035	21.009	5.335	0.022	0.148	N
PC	0.083	0.059	11.197	8.826	0.110	0.332	N
LC	-0.007	0.035	22.313	5.275	0.008	0.089	N

Linear function is: $Y = (m \pm \text{SEm}) X + (q \pm \text{SEq})$ where Y is the anatomical character, and X is the Mantle Length (ML).

the apparent isolation of the eastern and western populations have given rise to speculation about relationships among the populations (Zuev 1966, M R. Lipinski and Ch. M. Nigmatullin, pers. comm.). The present study does not support the concept of distinct taxa represented by the Gulf of Mexico/Caribbean and Tyrrhenian Sea populations. Although some differences were found in hectocotylus characters, most were not consistent enough to be statistically significant. We interpret these results to mean that the two populations studied are indeed conspecific.

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